POLLINATION IN LINARIA

WITH SPECIAL REFERENCE TO CLEISTOGAMY

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(WITH FOUR FIGURES)

I. POLLINATION BY INSECTS

The genus Linaria furnishes examples of adaptations to both cross- and self-pollination. Of the sixteen species given in KNUTH'S *Handbuch der Blütenbiologie*, nine are said to be visited by insects and may be pollinated by them. One, *L. origanifolia* DC., as observed by MACLEOD, is adapted to insects, but was not seen to use them. Four or five seem to be restricted to self-pollination, and all can also employ it. Some produce cleistogamous flowers, and as far as these can be of service, are compelled to pollinate in this way. *L. vulgaris* Mill. (as *Antirrhinum Linaria* L.) was the first to be observed and described. This was by CH. K. SPRENGEL in his book on the relations of flowers and insects, published in 1793. It was one of the first with which DARWIN experimented when preparing the material for his work on the effects of cross- and self-fertilization in the vegetable kingdom. An unexpected presentation of vigor in one of two beds of this species, planted for the purpose of determining some points regarding inheritance, led him to trials with this and other plants on the results of pollination.

Linaria is called a mellitophilous genus, since bees are the principal agents in the process, though in some species several other insects, especially Lepidoptera, share in the work. The honey, secreted by glands at the base of the ovary, flows into the spur of the flower, where it is stored and awaits the visits of insects with a proboscis long enough to reach it. It is therefore well adapted to visitors of this kind belonging to the class called Eutropic by LOEW.[1] The two pairs of anthers are placed at different heights, with the slender style and the stigma in the space between. These are brushed by the back of a bee crowding in to get the nectar in the spur, or by the longer proboscis of a lepidopter, and some of the pollen is removed

[1] LOEW, Einführung in die Blüthenbiologie 342, 345. 1895.

during the operation. That which was left on the stigma of the flowers by the entering and withdrawing of the bees was the extent of pollination as viewed by SPRENGEL. It was an aid to the plant in securing fertilization indispensable in the case of some, but the full significance in the economy of its life was left for others, especially for DARWIN, to show. SPRENGEL clearly describes the process in the text and figures illustrating *Antirrhinum Linaria*,[2] and in reading his book one wonders at the sagacity of the man so far in advance of his time. The relative position of anthers and stigma, coupled with their simultaneous maturing, can also, as stated by HERMANN MÜLLER, lead just as readily to self-pollination, and in the absence of visits by insects makes it the only possible means of fruitfulness.[3] The same relations hold in the case of the smaller flowers of *L. alpina* Mill., which MÜLLER investigated.[4]

The common toad-flax of Europe, *L. vulgaris*, has been naturalized in this country, and is most frequently seen along roadways or in waste grounds. Two native species are generally recognized, *L. canadensis* (L.) Dumort. and *L. floridana* Chapm. A third, *L. texana* Scheele, is made by some, but by others is considered a large-flowered form of *L. canadensis*. This seems to be the only one that has been studied with regard to its pollination. It is widely distributed, usually growing in dry locations, such as sandy or rocky ground. Its small flowers ally it more to *L. alpina* than to *L. vulgaris*, and like these it is adapted to pollination by insects. CHARLES ROBERTSON observed the flowers in Florida, and found that they were visited by bees, but more often by butterflies. He says of them: "The spur is very slender and the tube has become so contracted that bees can only insert their tongues, and butterflies cannot suck without touching the anthers and stigma. . . . . The palate, which in *L. vulgaris* permits the visits of bumble-bees only, seems to have lost its function, for it is so weak that it entirely fails to exclude butterflies or even flies."[5] Where I have noticed it in the dune region near Chicago,

[2] SPRENGEL, Das entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen 317. *pl. 17. figs. 5–11, 14, 18, 19.* 1793.

[3] MÜLLER, Die Befruchtung der Blumen durch Insekten 279. 1873.

[4] ———, Alpenblumen 275. 1881.

[5] ROBERTSON, Zygomorphy and its causes. III. BOT. GAZETTE 13:228. 1888.

it does not appear to be very extensively sought by insects, but species of Syrphidae may be seen flitting from flower to flower of this and of plants of *Krigia virginica* in blossom at the same time, perhaps as much in search of pollen as for their sweets.

MÜLLER examined other European species of Linaria with reference to this matter, among them *L. minor* Desf. and *L. arvensis* L. Their flowers are very small, but adapted, like *L. vulgaris* and *L. alpina*, to pollination by bees. As a weed in his garden at Lippstadt he "looked in vain" for visitors to *L. minor*, and *L. arvensis* was repeatedly watched in favorable weather in another station with a like result. Hence he concludes that they are restricted to self-fertilization. As the anthers burst at the same time the stigma matures, should a bee come for the nectar the flowers are ready for cross-pollination. This condition lasts only a short time; the stigma is soon covered with pollen, and self-fertilization is accomplished. Since MÜLLER cannot imagine that a flower, in all the peculiarities of its structure fitted for pollination by insects, should still be very exceptionally visited and crossed by their instrumentality, he concludes that we have in these plants a deteriorating descendant of an ancestor with larger and more striking flowers, in whose pollination bees as a rule took part.[6] He considers that the same is true of various other plants with diminutive or inconspicuous mellitophilous flowers which are now very rarely visited by bees, citing among others *Vicia hirsuta* Koch as a similar case, whose style bears unequivocal marks of arrested development, the brush being reduced to a dozen hairs at most.[7]

II. THE CLEISTOGAMIC CONDITION

It is only a step from this reduction of floral organs mentioned by MÜLLER to flowers so diminutive and constructed in such a way that they do not open at all, or the cleistogamic stage, in which self-pollination is the only means of securing fertility. Of the eight types of entomophilous flowers made by DELPINO, the sixth is that in which the anthers and stigmas are close together and included. Linaria answers these conditions, as must indeed be the case with

[6] MÜLLER, Weitere Beobachtungen III. Verh. nat. Vereins Rheinl. Westf. **39**:28. 1880.

[7] ———, *Ibid.* II. *Op. cit.* **38**:360. 1879.

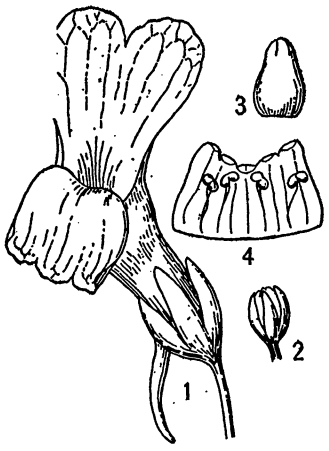
all cleistogamous flowers in respect of the proximity of the organs essential to fertility. It is these cleistogamous flowers I have mainly investigated. My attention was first called to them in 1905, when flowers of this character were found on *L. canadensis* growing upon the sandstone rocks at Oregon, Ill. They were quite inconspicuous. The minute corolla, when pushed off by the enlarging ovary, showed a faint tinge of violet on its upper margin, the main part being colorless. Since it was the middle of July, all traces of the sterile radical shoots had disappeared, as well as such flowers as are ordinarily found earlier in the season, if, indeed, they had been formed at all. The plants were generally small, the shortest mostly with simple stems. Some were branched, the tallest about 4^{dm} high. Since the species is well represented, though not abundant, on the sand dunes at the south end of Lake Michigan, there has been an opportunity to observe it each season since, and to note the different stages of development. The plants begin to blossom about the first of May and continue, in some form, the production of flowers till the middle or latter part of July, when the heat becomes too trying for them in the dry sand. On the larger plants there is a gradual diminution in the size of the flowers from the earliest, $6–8^{mm}$ long, with a diameter of limb of $8–12^{mm}$, till the cleistogamous stage is reached. In some plants of this character, this may occur in the early part of June. It is exceptional to find flowers which are relatively conspicuous during the later part of the life of the plant, and when found they are apt to be much reduced as compared with the earlier forms. The inflorescence being indefinite, the lengthening of the main stem and branches favors this progressive diminution. Plants that do not exceed 10 to 15^{cm} usually remain simple and are mainly restricted to cleistogamy. Plants taller than this commonly have flowers adapted to pollination by insects, though it must be rare in the smaller flowers, if done at all, when the limb of the corolla is but 3 or 4^{mm} in diameter, as MÜLLER found was the case with the small flowers he mentions.

Cleistogamy begins on stems not more than 2^{cm} high, which may be limited to a single flower at the tip, or perhaps lengthen enough to bear two or three. Flowers will appear on these diminutive stems as early as the larger petaliferous ones on the vigorous plants, the

two forms being synchronous, but on stems under different circumstances. They continue to increase in number on plants of this simple character until the stem ceases to lengthen or becomes mature, various heights being reached, but rarely more than 2^{dm}. Other slender and normally simple stems, usually not flowering at all till 12 to 15^{cm} high, bear as a rule small open flowers, and may continue to do so for some time, growing on till by progressive diminution of size the cleistogamous stage is reached. But the plants are apt to branch when 15 to 20^{cm} high, and bear the larger flowers on the main stem and branches that successively form. Two or three of these stouter stems often spring from the same root, forming a small cluster, with larger and more abundant radical shoots, the plant in all its features showing its greater vigor. In BRITTON and BROWN'S *Illustrated flora*, the statement is made under *L. canadensis:* "A dwarf form with no corolla is frequent." This evidently refers to the cleistogamous form. But the stage with no corolla is not confined to the dwarf plants. It was not on such that I noticed them at first, but on those which varied in height. In the dune region they may rise to 6^{dm} and bear the closed flowers in the later stages of growth. As the taller forms often branch quite freely, great numbers of capsules are borne, developing on the principal stem and branches at the same time and long after the ripened capsules lower down have opened and dropped their seeds. Since the branches ascend rather sharply, frequently rising well up to the level of the primary axis, a copiously branched plant, sometimes with fifteen to twenty members, may result. These have a bushy appearance, but they all produce the closed flowers before the plant dies, and manifest its ability to bear vast numbers of seeds.

The length of the corolla in the closed flowers is 1.2 to 1.6^{mm}. It is tubular, or sometimes slightly funnelform, but owing to the quite rapid growth of the ovary soon becomes enlarged at the base, and when pushed off is shaped more like an inverted funnel; or, if enlarged at the same time above, it has somewhat the form of an hour-glass. The limb is slightly irregular, the two-lobed upper lip being higher than the three-lobed lower, and overlapping it in the bud. In the illustration *fig. 1* shows an ordinary chasmogamous flower, *fig. 2* a cleistogamous flower, both enlarged five diameters, *figs. 3* and

4 a cleistogene corolla enlarged ten diameters, that of *fig. 4* displayed, the division being made between the two lobes of the upper lip. The style and stigma, if represented, would be between the two pairs of stamens as in the ordinary flowers, the stigma in this case closely pressed by the anthers when the parts are in place. The four stamens are apt to be present, and slightly didynamous. Sometimes a small protuberance at the base of the tube represents the spur. In the smaller chasmogamous forms, this may be reduced to a short sack or tooth, and usually decreases in size as the other parts diminish. But in some cases it remains relatively longer in comparison with the lessened tube and limb. I found no case of a cleistogene without a corolla. But as in other cases of cleistogamy it is easy to imagine the flowers represented by the calyx and the essential organs of fructification.



FIGS. 1–4.—*Linaria canadensis.* Fig. 1, petaliferous flower ×5; *fig. 2*, cleistogene flower ×5; *fig. 3*, corolla of cleistogene flower ×10; *fig. 4*, the same, displayed, ×10.

Depauperate as well as larger forms with cleistogamous flowers have been noted by others. RYDBERG, in his *Flora of the Black Hills*, mentions a *L. canadensis* collected at Custer as being "slender and depauperate, apparently with cleistogamous flowers. The same has also been collected in Nebraska."[8] The month given for RYDBERG'S collection is August. J. R. WEBSTER records cases observed by him at Milton, Mass., August, 1898. The plants were again noticed the next year, being "examined almost daily from April to October, and were seen to produce flowers abundantly which were all cleistogamous." They were observed by him in other localities, in which were also racemes which bore in addition fully developed flowers.[9] As the plants at Milton are said to reach the height of

[8] RYDBERG, P. A., Contrib. U. S. Nat. Herb. 3:517. 1896.

[9] WEBSTER, J. R., Cleistogamy in *Linaria canadensis.* Rhodora 2:168. 1900.

twenty to twenty-four inches and to produce branched racemes, "some of which were a foot or more in length," they were evidently of the larger forms, such as grow in the dune region in Indiana. But in their lack of chasmogamous flowers, they are somewhat different from any I have noticed there. The cases alluded to in his article as seen in "other localities" are more like those I have described. T. S. BRANDEGEE has likewise observed the plant about San Diego, Cal., "bearing cleistogamous flowers on the lower part of the main and the whole length of many side branches,"[10] apparently more like the larger forms here. Yet these statements from different sources indicate that the plant varies somewhat in its behavior in the respective localities, due perhaps to different environment.

Cleistogamy in Linaria is not confined to our wild toad-flax. It is one of the forty-four genera given in an article by KUHN in 1867 as producing examples with flowers of this character.[11] This list has been much increased since that date. KUHN does not give the name of the species, but probably refers to *L. spuria* Mill., whose peculiar florescence was described by EUGENE MICHALET in 1860.[12] MICHALET gives it as an example of a plant bearing hypogeous flowers. "These flowers," says DARWIN, "may be ranked as cleistogamic, as they are developed, and not merely drawn, beneath the ground."[13] It also has another peculiarity, according to MICHALET "infrequent in an annual plant," that of producing hypocotylous buds. Its lower leaves are opposite and much crowded. Two kinds of branches spring from their axils. Some of these, strong and often much elongated, spread over the surface of the ground; others short, slender, and much twisted, with small squamose leaves, gather in a bunch above the collar of the root, "all with a manifest tendency to bury themselves in the ground, especially the small hypocotylous branches which sometimes appear." Under suitable conditions they may penetrate the ground to the depth of 2 cm. On account of the

[10] BRANDEGEE, T. S., Cleistogamous flowers in Scrophulariaceae. Zoe 5:13. 1900.

[11] KUHN, M., Einige Bemerkungen über Vandellia und der Blütenpolymorphismus. Bot. Zeit. 25:67. 1867.

[12] MICHALET, E., Sur la floraison des Viola . . . . et du *Linaria spuria*. Bull. Soc. Bot. France 7:465. 1860.

[13] DARWIN, C., Different forms of flowers 325. 1877.

pressure to which they are subjected, the flowers are poorly developed, but otherwise show nothing peculiar in their structure. The corolla is crumpled and deformed, but "preserves even its natural color, with the two brown spots on its upper lip." The calyx alone loses its color. Fructification takes place regularly. MICHALET adds that the phenomenon can be produced at will by heaping earth around the lower part of the plant, this not interrupting the flowering of the covered portion. The treading of cattle and the pressure of wheels bring about the same result. As this plant of Europe and northern Africa is now introduced into this country, being, according to GRAY'S *New manual*, "occasional on ballast or waste grounds," an opportunity is provided for observing its behavior here. Another species of north Africa, *L. agglutinans* Pomel. var. *lutea*, belongs to this class of hypogeous plants, as observed by L. TRABUT in Algiers. It has cleistogamous flowers on shoots which spring from the stem near its base and ripen their fruit underground.[14]

III. RELATIVE ADVANTAGES OF THE TWO MODES

It is a distinct advantage to a plant growing under the conditions of *Linaria canadensis* to prolong its period of fruiting with a lessened demand on its supply of food. The environment is xerophytic. At Oregon it was the southern slope of a steep hill, fully exposed to the light and heat of the sun. The soil was sandy, and soon parted with any moisture that was supplied by rains and dews. The conditions in the dunes are similar, the slopes of sand hills or along paths and roadways in open sunny spots. The growth is usually scattered, though many plants may form a community, but the ground is not covered with a dense mat or bed as it commonly is by *L. vulgaris*. The slender stems provide but meager shade for the ground about their roots. In the early part of the season, or if it continues wet, the radical shoots form rosettes around the base of the stems, which protect the roots to some extent. In ordinary seasons these soon wither, and they may not be formed at all on plants which spring up later, being minute or wanting as in the smaller early plants. It is also a species poorly adapted to competition. When pressed by perennials, or by plants disposed to form a close stand, it soon disappears. And

[14] KNUTH, Handbuch der Blütenbiologie 32:113. 1905.

the plants associated with it, even if perennials, are not very sturdy competitors, but mostly of gregarious habit also. At Oregon they were chiefly *Lechea tenuifolia*, *Talinum teretifolium*, *Selaginella rupestris*, *Silene antirrhina divaricata;* in the dunes of Indiana, *Krigia virginica*, *Arabis lyrata*, *Viola pedata*, *Polygonella articulata*, and *Festuca octoflora*. But to whatever extent the time of fruit-bearing may be prolonged by cleistogamy, it is comparatively short in such habitats. It starts early, when there is little competition, and being an annual or fall-biennial, soon accomplishes its life-work.

That the cross-pollination of the earlier and larger flowers of *L. canadensis* must also be much to its advantage, in increase of vigor and productiveness, is evident from the nature of this process. This was clearly proven by DARWIN in his experimental work with cross- and self-fertilized plants. Of two beds of *L. vulgaris*, raised respectively from self-fertilized and crossed seedlings, those of the latter were seen to be much more vigorous. This led him to trials with this and other plants, the results of which are given in his book upon this subject. The case of Linaria needs only to be cited. As showing the vigor, "the naturally crossed plants were to the spontaneously self-fertilized plants in height, at least as much as 100 to 81." In regard to fruitfulness similar results came from the two modes of treatment, that of allowing or preventing the visits of bees. "The number of seeds in the capsules on the exposed plants to the average number in the finest capsules on the protected plants was as 100 to 14," or as expressed by him in a summary of plants so treated, the self-fertilized were "extremely sterile."[15] KNUTH is even more emphatic in stating that though self-pollination is possible and can occur spontaneously in *L. vulgaris*, it is of little consequence or without result.[16] In cases of this kind, where pollination from without and within takes place simultaneously, HERMANN MÜLLER thinks it probable that the former preponderates in its effects, and that the desired result is secured in this way.[17]

[15] DARWIN, C., Cross and self-fertilization in the vegetable kingdom 88, 89, 363. 1877.

[16] KNUTH, Blumen und Insekten auf dem nordfriesischen Inseln 111. 1894.

[17] MÜLLER, Befruchtung der Blumen 279.

IV. LIGHT AND HEAT AS FACTORS IN CLEISTOGAMY

The behavior of *Linaria canadensis* led to the conclusion that the gradual diminution in size of flowers was connected with the increase of heat, and perhaps of the light, to which they are exposed. Taking the larger plants as typical examples, the two features are in inverse proportion. This might be taken as a coincidence, but it seemed to be explained better as a coordination, and more in harmony with observations and experiments by others. In 1874 BOUCHÉ called attention to his observations that the diminution in the size of flowers and the production of cleistogamy depend in some plants on the decrease or increase of heat, in others on the decrease or increase of the length of the day. In the behavior of some, of which *Vinca rosea* L. is an example, the light acted favorably, the largest flowers being formed during the longest days, the smallest during the season of the shortest days. This seemed to depend on the light, since with a higher temperature after the longest days had gone by the decrease went on. In other cases cited by him, the decrease in size and production of cleistogamy are coordinated with the increase of heat and light, as if these acted unfavorably. As examples of this are the malvaceous plants, *Pavonia hastata* Spr. and *P. praemorsa* Willd. They begin to bloom at the end of May and show the phenomena of diminution and cleistogamy until the autumnal equinox, after which the flowers gradually increase in size till the beginning of winter or close of their floral season.[18] The case of the pavonias more closely accords with that of *L. canadensis*, as far as the floral season of the two coincide. But since, according to BOUCHE, the effects are not uniform, and may even lead to opposite results with different plants, there must be something in the plants themselves which causes the different response, or other environmental conditions must be taken into account. In the case of Linaria, I had associated it chiefly with the increase of heat which ordinarily occurs in summer, and the consequent diminution or more rapid removal of the moisture from the soil of such localities as the plants frequent. The equilibrium between absorption, either from the air or ground, and transpiration is disturbed. The smaller or cleistogamic flower, requiring less food, permits a husbanding of resources for the production of seed.

[18] BOUCHÉ, Gesells. naturf. Freunde 90, 91. 1874.

The vitality of the plant is lessened, but its ability to bear seed in abundance still remains. Economy in productive power results in a prodigality of the means to perpetuate. The waste, seeming or actual, is seen in the countless numbers of seeds which never have a chance to germinate. The scattered plants which annually appear show the need of this productiveness in order to obtain a few that can overcome the adverse conditions.

Aside from any effect which the increase of heat and light may have upon a plant in augmenting transpiration, and thereby making it advantageous to diminish the exposed surface, it is plain that the essential organs of reproduction are withdrawn from such effects far more in cleistogamy than in chasmogamy. As the name implies, these organs are hidden. But there is also a further tendency in many cases of cleistogamy to withdraw the perianth, or protective organs, from the direct effect of the sun's rays. *L. canadensis* is an example of the former tendency, *L. spuria* and *L. agglutinans* of the latter. These two species, as already stated, bend their peduncles down to produce their flowers or perfect their fruit beneath the surface of the ground. Other well-known examples of this are the milkworts, *Polygala polygama* Walt. and *P. paucifolia* Willd., bearing their flowers of this kind on subterranean runners. In the violets, where cleistogamy is so prevalent, the peduncles of the summer (usually apetalous) flowers are generally much shorter than those of the large petaliferous blossoms in spring. The flowers are more or less withdrawn from the light and shaded by the much enlarged leaves of the summer growth, or they may be borne on stems so shortened or declined as to be hidden under fallen leaves or buried in soft humus. The production of the closed flowers under such conditions may be due to a diminished intensity of light, as far as this has a bearing on them. Experiments like those of VÖCHTING show that the perianth of flowers is affected by decrease of light more than the reproductive organs. Chasmogamous flowers may be made cleistogamous in this way. The violets are quite variable in their relations to light, many of them being on the borderland between shade-loving and light-loving plants. The majority of our wild species bear their petaliferous flowers in the earlier part of their season of activity, those of the woods before they are strongly

shaded by the leaves of the trees and the taller plants of the forest floor, those of the field or open places before the grass or other growth overtops them. Their period of cleistogamy occurs when they are not subject to the strongest light. The one exposed to the greatest intensity of light, *Viola pedata* L., differs from most members of the genus in not having such flowers. Its season of blooming as well as environment correspond to those of *L. canadensis* when bearing its largest flowers. As a perennial, the violet has the advantage of drawing upon a supply of food stored in its much thickened root-stock. When this is diminished or too much exhausted, it goes on with the production of the enlarged summer-leaves, and by them elaborates another supply of food for storage. This may be a good explanation of its lack of the cleistogamy so general among its kindred, since it does not seem adequate to the work of bearing flowers and perfecting seed while producing the food for the future need of a xerophytic perennial. Under diminished temperature and favorable conditions of moisture its work of bearing petaliferous flowers may be resumed in late summer and autumn, but they are mostly smaller and much less developed than those of spring. *V. lanceolata* L. is also a species frequent in our dune region. It is a light-loving plant, often greatly exposed in the open sandy border of sloughs, but being hygrophytic has a supply of moisture on which to draw. Hence it passes its summer stage in the production of cleistogamous flowers, which continues long after that of the petaliferous has ceased. Yet it partakes of the general tendency among the violets, that of bearing them on shorter, more hidden stems, with the additional habit of producing them on stolens close to the ground. But *L. canadensis*, being an annual subject to xerophytic conditions, cannot draw on such resources as these two violets have. The development of its cleistogamous flowers evidently depends on its relations to heat and moisture more than on those of light.

V. DEGENERACY IN FLOWERS OF LINARIA

In *L. canadensis* is found an example of a plant passing through decadent stages to the condition of cleistogamy. The slight irregularity of limb and the occasional remnant of a spur show degeneracy, even if the smaller and varying intermediate forms of flowers were

not present. It has already been stated that MÜLLER looked upon *L. minor* and *L. arvensis*, and small-flowered species of Vicia, as examples of plants which had descended from those adapted by their floral structure to pollination by insects. In the plant we are considering, this process is epitomized. Pollination by the help of insects takes place in flowers of an inflorescence which gradually undergoes such changes in a single season as to preclude it. The process of reduction is seen in actual working, and it may be that such flowers, rather small at best, are on the way to a stage where visitation by insects will cease. Yet one cannot regard the explanation as entirely valid. By the very principle of adaptation here invoked, the opposite might come true; that is, visits by insects, frequently repeated and continued for a long period of time, would finally produce flowers better suited to their work. Irregularity of floral structure is regarded as such an adaptation, and to some extent has been explained by it. A causal relation between the two is traced. In DARWIN'S list of genera with cleistogamic flowers, thirty-two of the fifty-five he gives have the flowers in their most advanced stage irregular. He says that this "implies that they have been especially adapted to fertilization by insects."[19] Without pressing such explanations too far, it is seen in the case of the wild toad-flax that provision for cross-fertilization is made in the structure of flowers borne simultaneously with the cleistogamous, or at an earlier date, on the same plant. In this there is insured to the species the present means of invigorating its life, the primary benefit to be derived from it, whether it be a waning or waxing advantage.

CHICAGO

[19] DARWIN, C., Different forms of flowers 339.